DISCARD THE NAMES THERIODONTIA AND ANOMODONTIA: A NEW CLASSIFICATION OF THE THERAPSIDA

By

L. D. Boonstra

South African Museum, Cape Town

(With 2 figures)

[*MS. accepted* 25 *January* 1972]

Contents

	PAGE
Introduction	315
Diagnoses	318
Diagnoses of the higher taxa	322
Summary	334
References	334

Introduction

Since the discovery of certain Permian reptiles in Russia and South Africa in the early thirties of the 19th century showing some characters of a mammalian nature and their first descriptions by Kutorga in 1838 and Owen in 1844 numerous attempts have been made by various authors to fit them into the taxonomic system in such a way as to indicate in what manner these reptiles could be considered related and ancestral to the mammals.

I have found the historical study of the various classifications proposed by authors most interesting and illuminating and was tempted to publish a detailed historical review, but on second thoughts have decided that confining myself to the essentials of the ever increasing precision of the phylogenetic views would be more important and valuable and satisfying.

At the present time we know over 300 recorded genera of 'reptiles' which possess to varying degrees characters indicating a development in mosaic pattern in a general mammalian direction.

For this assemblage of 'reptiles' we have the name Therapsida coined by Broom in 1905.

In the present state of our knowledge this group as a whole appears to have evolved from captorhinomorph and sphenacodontid precursors.

The oldest known therapsids, from low down in the Permian, consist of an assemblage in which discrete lines of development are clearly evident.

For these lines of development we have the following denominations available:

1. Anomodontia (Owen 1859)
2. Dicynodontia (Owen 1860)

Ann. S. Afr. Mus. **59** (11), 1972: 315–338, 2 figs.

3. Cynodontia (Owen 1860)
4. Theriodontia (Owen 1876)
5. Dinocephalia (Seeley 1895)
6. Gorgonopsia (Seeley 1895)
7. Therocephalia (Broom 1903)
8. Scaloposauria (Boonstra 1953)
9. Phthinosuchia (Romer 1961)
10. Eotitanosuchia (Boonstra 1963)

There exists strong evidence that the Dinocephalia and Gorgonopsia evolved through the Eotitanosuchia from common sphenacodontid ancestors of the morphological habit such as that of the genus *Haptodus*. Taxonomically there may thus be some reason to coin a higher denomination to include the Eotitanosuchia, Gorgonopsia and Dinocephalia in order to indicate their consanguinity. Both these sublines of development, each showing the development of certain mammalian characters, became extinct—the Dinocephalia at the end of the Middle Permian and the Gorgonopsia at the end of the Upper Permian.

The dinocephalian line shows certain stages of development. The most primitive stage is represented by a group of animals for which the name Eotitanosuchidae has been used by Tchudinov (1960).

Ascending directly from the Eotitanosuchidae is the group Brithopodidae (Efremov 1954). From the Brithopodidae two higher groups arose dichotomously, viz. the Anteosauridae (Boonstra 1954) and the Titanosuchidae (Broom 1903). From the Titanosuchidae three higher stages diverged, viz. the Tapinocephalidae (Owen 1876), the Styracocephalidae (Haughton 1929) and the Estemmenosuchidae (Tchudinov 1960).

The Gorgonopsia line shows the following stages of development represented by groups with the following denominations:

Phthinosuchidae (Efremov 1954)
Hipposauridae (Watson & Romer 1956)
Gorgonopsidae (Lydekker 1890)
Burnetiidae (Broom 1923)

The dicynodontian line arising from unknown but probably sphenacodont ancestors has as its oldest known representative the genus *Otsheria* from which I have proposed the group name Otsheriidae (Boonstra 1963). Diverging from this base there are the short-lived groups Venyukoviidae (Efremov 1940) and Galeopsidae (Broom 1912) and the longer lived but also sterile line of the Dicynodontia (Owen 1860) which split up into the Endothiodontidae (Lydekker 1890) and Dicynodontidae (Owen 1876) from which arose the Kistecephalidae (Seeley 1895), Lystrosauridae (Broom 1903) and the Kannemeyeriidae (Von Huene 1948).

The third line, first encountered in the Middle Permian is that of the Therocephalia (Broom 1903). Arising from as yet unknown but probably sphenacodont ancestors they formed an important group of carnivores during *Tapinocephalus* zone times, when they had already developed diverging branches with the following denominations:

Pristerognathidae (Broom 1906)
Lycosuchidae (Broom 1910)
Alopecodontidae (Broom 1932)

This line, strongly developed in the Middle Permian, became extinct at the end of the Upper Permian with the last off-shoots represented by the Whaitsiidae (Haughton 1918) and the Euchambersiidae (Broom 1931).

The last line, also beginning in the Middle Permian, with a few inadequately known forms, is that of the Scaloposauria (Boonstra 1953). This line may have arisen from the therocephalian line during the Lower Permian and is certainly closely related. Both the therocephalian and scaloposaurian lines apparently arose from some earlier sphenacodonts, but we have no certain indication of this as we have in the first line where a *Haptodus*-like form is indicated.

Commencing in the *Cistecephalus* zone and continuing to the top of the *Cynognathus* zone we find the Bauriamorpha (Watson 1917) which are generally considered to have arisen from the earlier ictidosuchian Scaloposauria.

Also commencing in the *Cistecephalus* zone and continuing into the Red Beds we have a final branch—the Cynodontia (Owen 1860) culminating in the near-mammals—the Tritylodontia (Simpson 1925). If the Cynodontia are not a parallel branch to the Scaloposauria, both to be derived from primitive therocephalians, then one must postulate a direct and separate derivation from some earlier sphenacodont.

From the foregoing it is clear that I think that we have three main branches of Therapsida.

An older view was that there were two main branches which have been labelled:

Anomodontia (Owen 1859) and
Theriodontia (Owen 1860)

Anomodontia

Although Owen initially in 1859–60 clearly intended the terms Anomodontia and Dicynodontia to have as type, *Dicynodon*, he later included some theriodonts.

Since then the term Anomodontia has had a chequered career, being used by authors to include a variety of other forms manifestly un-*Dicynodon*-like. The term Anomodontia being thus misused it would be pragmatic to drop it altogether and rather retain the name Dicynodontia solely for those forms showing a *Dicynodon*-like structure as originally intended by Owen.

Theriodontia

In 1860 Owen coined the term Cynodontia with *Galesaurus* as the type and included it as a 'family' of his Anomodontia. In 1876 Owen introduced the term Theriodontia for the same genera included in his former Cynodontia, apparently to supersede the latter name. As Owen included genera now considered as Gorgonopsia and others as Cynodontia in his Theriodontia, and Watson recently also the Titanosuchia, which three groups are now known to lie on different lines of development, the term Theriodontia unites incompatible groups and should be dropped.

Deciding to discard the names Anomodontia and Theriodontia because they each bracket together lines of development which, as I have indicated, are not nearly related, it appears necessary to coin three new names for the three main branches of the Therapsida, and to include as subdivisions of each of these three new denominations those groups which are in fact closely related.

For the first of these branches I propose the name Alphatherapsida to include the subdivisions Eotitanosuchia, Dinocephalia and Gorgonopsia.

For the second branch—Betatherapsida—to include only those forms related to *Dicynodon*.

For the third branch the name—Gammatherapsida—to include those fertile groups directly related and finally leading to the first mammals, viz. Therocephalia, Scaloposauria and Cynodontia.

Diagnoses

ALPHATHERAPSIDA

Dentition primitively carnivorous with pointed incisors, canines and postcanines adapted for snatching and tearing out flesh without cutting or chewing. Short-lived side branches with dentition transformed to herbivorous talon and heel teeth adapted for piercing and crushing without cutting and chewing.

Choanae anteriorly situated with air passage without bony ventral floor to partition it off during feeding.

The temporalis primitively originating from under surface of skull roof and inserted in the adductor fossa and on the upper edge of the dentary.

In the gorgonopsian branch the insertion was improved by the precocious development of a coronoid process on the dentary. Here we thus have a primitive origin coupled with an advanced insertion.

In the dinocephalian branch the origin of the temporalis shifts away from the under surface of the skull roof to the lateral surface of the intertemporal bones, but no coronoid process is developed. Here we thus have an advanced origin coupled with a primitive insertion. The later pachyostosis bedevils this aspect. The postdentary bones of the mandible are persistently well developed due to their retaining the primitive insertion of the adductors which exerted a greater horizontal than vertical pull, with the joint a simple hinge. But in the herbivorous forms a fore-and-aft motion allows for a crushing bite.

Concomitant with the primitive carnivorous jaw-mechanism the locomotory apparatus is of a crawling habit with sprawling limbs and little upraising of the body and only slightly reduced digital segments.

In the braincase the sphenoidal complex is very well ossified, but the prootic is feebly ossified, thus leaving a wide gap in the lateral wall with a loose standing unwidened epipterygoid. In the pachyostotic Dinocephalia the gap in the lateral wall is greatly reduced, but the narrow epipterygoid remains uninvolved.

In the Alphatherapsida the gorgonopsian branch has its characteristic structures developed early and these are retained, with only insignificant variations, throughout its span of life, notwithstanding that they survived to the end of the Upper Permian.

The dinocephalian branch commencing as a primitive carnivorous group early in its history, develops herbivorous twigs but the whole branch is short lived and unprogressive and is soon cut short by the pathological pachyostosis.

BETATHERAPSIDA

Dentition herbivorous, primitively with a series of marginal teeth, later with marginal teeth in part or wholly replaced by horny sheaths. Choanae shifted moderately posteriorly, with part of air passage with bony partition, separating it from buccal cavity, formed by plates of the premaxilla.

The jaw adductors highly specialized, particularly in their origins, with concomitant great lengthening of the temporal fossa and the development of a unique triradiate squamosal, and everted zygoma accompanied by a lengthened sliding articular facet allowing fore-and-aft sectorial movement of the jaw when feeding, insertions tending to shift on to the outer face of the dentary.

The postdentary bones unreduced.

Feeding on upland plants (except lystrosaurs and Kistecephalidae) the locomotor apparatus is adapted for a more upright walking gait, with an acromion process, greatly enlarged anterior iliac process, obturator foramen and reduced digital segments. In the braincase the sphenoidal complex is very well developed and situated far anteriorly; the prootic short, thus leaving a very long gap in the lateral wall, with a loose standing slender epipterygoid.

Notwithstanding its long span of life this group remained stationary on its early achieved developmental niveau. What variations arose were quite insignificant, initiating nothing phylogenetically fertile.

GAMMATHERAPSIDA

Dentition primitively carnivorous, but variations commence quite early, viz. reduction of postcanines (in lycosuchids and whaitsiids); development of additional precanines (in alopecodontids and Scaloposauria); tricuspid sectorial postcanines arose (in some Scaloposauria and some Cynodontia); grinding surfaces developed on postcanines (in some Scaloposauria and Cynodontia); differentiation into 'premolars' and 'molars' (in Cynodontia). Thus the primitive snatching and tearing dentition became adapted to cutting and grinding with a process of chewing.

Primitively the choanae were anteriorly situated, but concomitant with the developing of a chewing habit the choanae shifted backwards with the development of a secondary bony palate partitioning off the air passage from the buccal cavity during the process of mastication.

The temporalis originated from the lateral face of the intertemporal bones and inserted on the coronoid process.

Primitively, where the posterior mandibular bones are still well developed, the superficial masseter inserted on the reflected lamina of the angular and the internal pterygoid wrapped round the ventral edge of the angular. But in the cynodonts part of the superficial masseter inserted on the postero-ventral corner of the dentary and the internal pterygoid also partly moved on to the inner face of the corner of the dentary, which resulted in a reduction of the function and thus the size of the angular.

With the pull of the jaw muscles having strong horizontal components in the early forms the posterior mandibular bones remained strong to withstand the strain on the jaw joint. But with the jaw-closing muscles developing less horizontal and greater vertical pull the strain on the jaw joint decreased with a resulting decrease in size of the posterior mandibular bones.

With the increased strain on the dentary, due to its capturing some of the muscle insertions from the posterior bones, it developed a very large coronoid process and a prominent angle and, extending further and further posteriorly, in the final stages made contact with the squamosal to form a double jaw joint.

In the locomotor apparatus a more upright walking gait is developed with a reduction of the phalanges to 2,3,3,3,3 in all but the early cynodonts where the 4th and 5th digits have 4 segments.

Primitively with pubic foramen, advanced with obturator foramen. Primitively without, advanced forms with, infra-spinatus fossa.

In the braincase the sphenoidal complex is primitively not well ossified, but moderately so in some advanced forms. Primitively the prootic is feebly developed, but in advanced forms extends anteriorly to meet the epipterygoid.

Primitively the epipterygoid is usually slender but broadened in the primitive lycosuchids. In some advanced forms it is greatly broadened and meeting the prootic enters into the sidewall of the braincase (cynodonts).

Postorbital bar primitively well developed as also in some advanced forms but in some others it becomes weak and even incomplete.

Occipital condyle primitively single (tripartite), in advanced forms double and formed by the exoccipitals. Primitively with suborbital fenestra, but sometimes reduced, large in Scaloposauria, absent in Cynodontia.

In contrast to the Alphatherapsida and Betatherapsida the Gammatherapsida were a very versatile group in which developments, besides leading into a number of early as well as later blind alleys, produced very progressive parallel branches all in a general mammalian direction, with the procynosuchid–galesaurid–tritylodont branch most probably including the actual ancestors of the first mammals.

SYNAPSIDA

The term Synapsida (Osborn 1903) has by all recent students been used with the taxonomic rank of Subclass to include those vertebrates popularly known as the mammal-like reptiles. These animals possess a mosaic of characters some of which pertain to the Class Mammalia and others to the Class Reptilia.

They are thus neither true mammals nor true reptiles and do thus not fit into the Class Mammalia or into the Class Reptilia.

I thus support those recent authors who have proposed that the name Synapsida should have the rank of a separate Class.

The Class Synapsida would then include the two Subclasses Pelycosauria and Therapsida.

For the Subclass Therapsida I propose the following classification:

Subclass	Superorder	Order	Suborder	Family
Therapsida	Alphatherapsida	Eotitanosuchia		Eotitanosuchidae Phthinosuchidae Rubidginidae
		Dinocephalia	Brithopia	Brithopodidae Anteosauridae
			Titanosuchia	Titanosuchidae Tapinocephalidae Styracocephalidae Estemmeno-suchidae
		Gorgonopsia		Hipposauridae Gorgonopsidae Burnetiidae
	Betatherapsida	Venyukovioidea		Otsheriidae Venyukoviidae ? Dromasauridae
		Dicynodontia		Endothiodontidae Dicynodontidae Kistecephalidae Lystrosauridae Kannemeyeriidae
	Gammatherapsida	Therocephalia		Pristerognathidae Lycosuchidae Whaitsiidae
		Scaloposauria	Ictidosuchia	Alopecodontidae Ictidosuchidae Scaloposauridae

Subclass	Superorder	Order	Suborder	Family
Therapsida (continued)	Gammatherapsida (continued)	Scaloposauria (continued)	Bauriamorpha	Bauriidae Ericiolacertidae
		Cynodontia	Procynosuchia	Procynosuchidae Galesauridae ? Silphedestidae
			Cynognathia	Cynognathidae Diademodontidae Chiniquodontidae Traversodontidae
			Tritylodontia	Tritylodontidae Trithelodontidae Diarthrognathidae

Diagnoses of the Higher Therapsid Taxa

SUBCLASS THERAPSIDA

Advanced synapsids of the Permian and Triassic. There is strong evidence that one therapsid superorder, at least, was directly derived from sphenacodont pelycosaurs, but the derivation of the other two superorders from sphenacodonts, although very probable, is less certain. The therapsids include the direct ancestors of the mammals.

Further advanced than the pelycosaurs in that: the pterygo-basicranial joint is no longer freely movable; a longitudinal girder is developed, the interpterygoid vacuity is never widely open but partly or completely closed; the squamosal is outflaring with a posterior face; there is no supratemporal; the lacrimal never reaches the nostril and the maxilla is deep.

At the beginning of the Middle Permian the therapsids had already developed in diverse directions each showing a lesser or greater acquisition of certain mammalian characters.

Of the three main branches one became successfully adapted and dominated the scene during the Middle and Upper Permian, comprising herbivores and their predatory carnivores, but proved sterile; a second branch of herbivores became adapted to their special niche, waxed exceedingly and very successfully maintained themselves to near the end of the Triassic when they died out without issue; the third branch, already well established at the beginning of the Middle Permian, firstly as predators and later developing herbivorous side branches, developed more and more in the mammalian direction, with one or more twigs producing the first mammals late in the Triassic.

SUPERORDER ALPHATHERAPSIDA

Permian therapsids a stage further developed than the early Permian sphenacodonts from which they arose, not leading to mammals.

The intertemporal skull table is primitively broad and flat, with the posterior flange of the postorbital lying horizontally in the dorsal skull roof (but modified in some Dinocephalia) and reaching the squamosal; the postorbital bar is always complete.

The lower jaw primitively without a prominent coronoid process (but present in Gorgonopsia), the dentary always strong, but without a definite postero-ventral angle; the postdentary bones always well developed.

The quadrate is primitively robust with the quadrate ramus of the pterygoid strong (except in Gorgonopsia).

Primitively with simple conical incisors, canine and postcanines (but modified in some *Dinocephalia*) and palatal teeth on the pterygoid and palatine.

There is no secondary palate and no suborbital fenestra.

The epipterygoid is slender and does not enter the sidewall of the braincase; the prootic is weakly developed with a free anterior edge; the sphenoidal complex is well ossified.

The postfrontal is well developed; the dorsal premaxillary process is long (but short in Gorgonopsia).

A pineal foramen is always present.

The occipital condyle is single.

ORDER EOTITANOSUCHIA

The most primitive therapsids descending from sphenacodonts, with all the primitive characters listed in the diagnosis of the superorder Alphatherapsida of which they are the morphological ancestors.

Family **Eotitanosuchidae**

Eotitanosuchidae with the squamosal not extending into the intertemporal skull roof and the primary palate closed.

Family **Phthinosuchidae**

Eotitanosuchians with the squamosal developing a lappet entering the intertemporal skull roof and the primary palate with a median cleft.

Family **Rubidginidae**

Younger relict eotitanosuchians with a short series of serrated postcanines and a small temporal fenestra.

ORDER GORGONOPSIA

Middle and Upper Permian alphatherapsids descending from eotitanosuchians, which have developed a prominent coronoid process; the quadrate posteriorly situated is reduced in size and the quadrate ramus of the pterygoid is lightly built; the dorsal process of the premaxillary is shortened; a preparietal is developed. Extinct at the end of the Permian leaving no descendants.

Family **Hipposauridae**

Primitive gorgonopsians with a very broad intertemporal skull roof; small temporal fenestra, deep suspensorium, fairly long postcanine series, with the dorsal skull contour strongly curved.

Family **Gorgonopsidae**

Intertemporal skull roof somewhat reduced in both earlier and later forms, but in the latter sometimes secondarily greatly widened; large temporal fenestra, fairly shallow suspensorium, postcanine series reduced, gape of jaws in some Upper Permian forms enormous with very strong canines.

Family **Burnetiidae**

Later aberrant gorgonopsians with very wide intertemporal region, reduced temporal fenestra, dentition reduced with weak teeth; with pachyostotic thickening of roofbones of skull in the form of bosses and ridges.

ORDER DINOCEPHALIA

Early alphatherapsids derivable from an eotitanosuchian niveau and die out without issue at the end of the Middle Permian; with basically primitive structure obscured in some branches by pachyostosis and some abortive specializations.

Width of intertemporal skull table reduced, sometimes greatly so, but secondarily greatly widened where the pachyostosis is great, temporal fenestra moderate to large except where secondarily reduced by the pachyostosis.

No coronoid process on the dentary; primitively with a carnivorous dentition of simple conical teeth, later specialized carnivorous with an early development of a herbivorous branch and intermeshing of some or all the upper and lower batteries.

The quadrate robust, as also the quadrate ramus of the pterygoid; quadrate shifting anteriorly.

Dorsal process of the premaxillary long to very long.

SUBORDER BRITHOPIA

Primitive dinocephalians linked to the eotitanosuchians and morphologically ancestral to the other dinocephalian groups.

The intertemporal skull roof reduced in width with the posterior process of the postorbital lying at a slant down from the horizontal; the temporal fenestra large.

The dentition carnivorous, with the incisors tending to lengthen and the postcanines becoming reduced; the lower and upper incisors and canines intermesh.

Palatal teeth primitively well developed, later practically confined to the palatine.

Quadratojugal never a surface bone.

With no or little general pachyostosis.

Dorsal process of the premaxillary moderately long.

Family **Brithopodidae**

Primitive brithopians with a fairly long postcanine series; incisors not greatly lengthened; postfrontal not bulbously swollen and no other pachyostosis; quadrate with little anterior shift; moderate outflaring of squamosals. Palatal teeth well developed.

Family **Anteosauridae**

A stage further advanced than the brithopids. Postcanine series reduced, incisors greatly lengthened. Postfrontals becoming greatly bulbously swollen and the skull roof moderately pachyostosed. Strong outflaring of squamosals, especially posteriorly.

Palatal teeth reduced, practically confined to the palatine.

SUBORDER TITANOSUCHIA

Advanced dinocephalians derived from a brithopid niveau.

The intertemporal region reduced in width, sometimes to a narrow sagittal crest, but secondarily greatly to enormously widened where the pachyostosis is great; the temporal fenestra large to very large but secondarily greatly reduced.

The dentition is herbivorous, initially with a large conical canine and with only the incisors developing a talon and heel; later the canine is not distinguishable as such and all the marginal teeth develop a talon and heel; the postcanine series always very long. Palatal teeth practically absent.

Quadratojugal sometimes a surface bone.

The pachyostosis is moderate to enormous.

Family **Titanosuchidae**

Primitive titanosuchians developed from a brithopid level and indicating the morphological level from which the tapinocephalids arose.

The intertemporal width reduced with a low thick sagittal crest, posterior process of the postorbital reduced, temporal fenestra fairly large, but squamosals not outflaring.

Strong incisors with piercing talon and crushing heel and large conical canines, a long series of spatulate postcanines, which do not intermesh as do the incisors and canines of the two jaws. No palatal teeth.

Moderate pachyostosis.

Family **Tapinocephalidae**

Specialized titanosuchians derived from a titanosuchid level.

The intertemporal region very variable, mostly of moderate width, sometimes with a sharp sagittal crest, in one subfamily enormously broadened as a result of the excessive pachyostosis; temporal fenestra large to greatly reduced.

All the marginal teeth with talon and heel, upper and lower battery intermeshing.

Pachyostosis light to great.

Family **Styracocephalidae**

Middle Permian aberrant titanosuchians. Intertemporal region very broad, but temporal fossa roomy with posteriorly flaring squamosal; pachyostosis in the form of 'horns' and bosses.

Weak conical incisors and canine and a long series of postcanines; palatal teeth very well developed, even on the vomer.

Family **Estemmenosuchidae**

The 'horns' situated on the frontals, and directed dorsally, whereas in the Styracocephalidae the 'horns' are formed by the tabular and directed posteriorly. Otherwise with features very similar to those of the Styracocephalidae.

SUPERORDER BETATHERAPSIDA

Permian and Triassic therapsids on a developmental niveau far above that of the early Permian sphenacodonts, not leading to mammals.

The intertemporal skull table is primitively reduced in width, but flat, becoming narrow and later developing a sagittal crest, but secondarily widened in the Kistecephalidae; the posterior process of the postorbital inclined downwards from the horizontal and reaching the squamosal, later reduced; the postorbital bar is always complete.

The lower jaw without a coronoid process of the dentary and without a coronoid bone; the dentary always strong without a postero-ventral angle; the postdentary bones well developed. The quadrate is robust lying low down on a pedicel of the uniquely triradiate squamosal, and the quadrate ramus of the pterygoid is weak. Primitively with a modified set of marginal teeth in both jaws, which very early are radically reduced and sometimes wholly lost and replaced by horny sheaths; there are no palatal teeth.

The premaxillaries, primitively paired but later fused, develop plates to form a unique type of secondary palate and the choanae are shifted posteriorly; primitively the maxilla and palatine have no inward palatal growth but later extend palatally but never meet below the air passage. The epipterygoid is slender and does not enter the sidewall of the braincase; the prootic is weakly developed with a free anterior edge; the sphenoidal complex is well ossified and lies far anteriorly.

The postfrontal is primitively well developed but reduced later; the dorsal premaxillary processes are primitively paired and long, later fused and short.

A pineal foramen present; preparietal primitively absent, later present. The occipital condyle is single. There is a fenestra in the mandible between the dentary and angular.

ORDER VENYUKOVIOIDEA

Primitive betatherapsids not directly linked to the sphenacodonts, leading to the higher Dicynodontia.

The width of the intertemporal region is reduced, without sagittal crest and the temporal fenestra is short, the jugal has a large entry into the zygoma which is not strongly everted.

The dentition consists of a well-developed series of bluntly conical marginal teeth on the premaxilla, maxilla and dentary.

No inward growth of palatine and maxilla and the posterior part of the palate is thus primitive, except that the lateral ramus of the pterygoid is somewhat or much reduced.

The premaxillaries are not fused and have a long dorsal process; the septomaxilla is largely superficial, the postfrontal is well developed and there is no preparietal.

Family **Otsheriidae**

The incisors are enlarged, the choana is short, the palatine does not meet the premaxilla; the lateral ramus of the pterygoid is still prominent, the lacrimal is short and there is no pachyostosis.

Family **Venyukoviidae**

The incisors are enlarged, the choana is long; the palatine meets the premaxilla; the lateral ramus of the pterygoid is much reduced; the lacrimal is long; there is some pachyostosis.

Family **Dromasauridae**

The dentition consists of a series of isodont marginal teeth or the jaws are edentulous; the temporal fenestra is very short and deep.

ORDER DICYNODONTIA

Advanced betatherapsids morphologially derivable from *Otsheria*; a long-lived order, rich in species varying in minor characters with a single main theme and phylogenetically sterile.

The intertemporal region reduced in width, sometimes very much so, but is secondarily widened in one aberrant family; the sagittal crest feeble to very high or wholly absent. The temporal fenestra is very long and the jugal is practically ousted from the zygoma by the squamosal which is uniquely everted.

The marginal teeth are greatly modified, there are never any incisors; an upper conical canine present or absent; postcanines present or absent and when present shifted medially and variously disposed.

Palatal flanges of the palatine and maxilla tending to grow inwards to form a variable open trough for the air passage; the lateral ramus of the pterygoid is lost.

The premaxillaries are fused and the dorsal process is short; the septomaxilla tending to shift interiorally; the postfrontal is primitively present but is lost in later forms; a preparietal is developed.

Family **Endothiodontidae**

With postcanine teeth, number and disposition very variable, canines present or absent, with a postfrontal.

Family **Dicynodontidae**

Without postcanine teeth, canines present or absent, the postfrontal is frequently absent.

Family **Kistecephalidae**

The intertemporal region is secondarily greatly widened, without sagittal crest, edentulous, without canines, without pre- and postfrontals and pre-parietal.

Family **Lystrosauridae**

Without postcanines and canines usually present, postfrontal present, nares shifted posteriorly and premaxilla lengthened.

Family **Kannemeyeriidae**

Very high sagittal crest; depression leading into pineal foramen.

SUPERORDER GAMMATHERAPSIDA

Permian and Triassic therapsids probably derived from Early Permian sphenacodonts and including the immediate ancestors of the mammals.

The intertemporal skull table narrow, usually with a sagittal crest, but secondarily widened in one late family; the postorbital is reduced and never reaches the squamosal; the postorbital bar primitively and usually complete, but incomplete and even wholly absent in some advanced forms.

The dentary primitively and usually with a prominant coronoid process, strong and finally greatly enlarged with a strong postero-ventral angle and making contact with the squamosal; the postdentary bones primitively well developed but greatly reduced in some advanced groups.

The quadrate small, with weak to incomplete quadrate ramus of the pterygoid.

Primitively with carnivorous dentition of simple conical teeth, later very variable, often with accessory cusps in the postcanines and in some advanced forms with highly elaborated crowns of a mammalian nature.

Primitively without secondary palate, in later groups incipient in various ways, to incomplete, and finally fully developed in mammalian fashion.

The epipterygoid is primitively slender and remains so in many forms, but is widened in some early forms and in advanced forms very broad and incorporated into the sidewall of the braincase; the prootic is primitively weakly developed, but later growing forwards meets the epipterygoid (alisphenoid) suturally; the sphenoidal complex is usually not well ossified.

The postfrontal small or absent.

The occipital condyle single in earlier forms, later becomes notched and finally with double condyles formed by the exoccipitals.

ORDER THEROCEPHALIA

Middle to Upper Permian gammatherapsids; initially primitive but with a wide gap between them and their sphenacodont precursors; with a degenerate family in the Upper Permian; relation to higher gammatherapsids is uncertain.

The intertemporal region is narrow with a reduced postorbital; the postorbital bar always complete; pineal foramen always present; dentary with a well-developed coronoid process and the postdentary bones well developed; no prominent postero-ventral angle to dentary.

Primitively without secondary palate but aberrantly incipient in the Upper Permian family.

Epipterygoid slender or widened but never incorporated in the sidewall of the braincase.

Dentition primitively carnivorous with a long postcanine series, later greatly reduced to lost, always uncusped. Postfrontal small or absent, suborbital fenestra large in earlier forms but reduced to absent in later forms.

The occipital condyle is always single.

Family **Pristerognathidae**

Middle Permian therocephalians with a well-developed carnivorous dentition with a single canine; no secondary palate, epipterygoid slender, postfrontal small, suborbital fenestra large.

Family **Lycosuchidae**

Middle Permian therocephalians with a well-developed carnivorous dentition, with double canines; no secondary palate, epipterygoid widened; postfrontal small, suborbital fenestra large.

Family **Whaitsiidae** (including **Lycedeopsidae** and **Euchambersiidae** as subfamilies)

Upper Permian therocephalians with reduced dentition, postcanines feeble, few or wholly absent, lower incisors sometimes absent, aberrant development of an incipient secondary palate, epipterygoid widened, suborbital fenestra large to small or absent, dentary scimitar-shaped with postdentary bones not robust.

ORDER SCALOPOSAURIA

Middle Permian to Lower Triassic gammatherapsids, probably independently derived from sphenacodonts with a considerable gap; fairly primitive in the Middle Permian, but advanced in the Upper Permian and Lower Triassic; relations to cynodonts uncertain.

The intertemporal region is usually narrow with a sagittal crest, but widened in one family with loss of crest; the postorbital bar is slender and complete or incomplete; the postorbital is sometimes greatly reduced or even absent; the jugal spur of the postorbital bar is usually present but absent in a few forms; the pineal foramen is sometimes absent.

The coronoid process of the dentary is strong, feeble or absent; there is no prominant postero-ventral angle to the dentary; the postdentary bones are well developed or weakened. A secondary palate is primitively absent, later incipient to well developed. The epipterygoid is mostly slender but sometimes widened and partially included in the sidewall of the braincase in one form.

A prominent canine is usually retained but sometimes not recognizable as such, accessory small canines are usually present, maxillary teeth usually numerous and the postcanines variable, being simple, cusped or with transversely widened crowns.

The suborbital fenestrae are always well developed, the postfrontal is reduced or absent.

The occipital condyle is initially single but later sometimes incipiently double.

SUBORDER ICTIDOSUCHIA

Mostly Permian scaloposaurians just extending into the Triassic; the intertemporal region is usually narrow but later widened in one family, the postdentary bones are weakened and the dentary lightly built; the secondary palate is primitively absent, sometimes incipient but never complete, the epipterygoid is slender but in one case partially enters the sidewall of the braincase.

Family **Alopecodontidae**

Primitive Middle Permian ictidosuchians close to the contemporary therocephalians.

The intertemporal region is narrow with a sagittal crest; the postorbital bar is complete, the coronoid process is strong, the dentary robust and the postdentary bones well developed; there is no secondary palate.

Dentition carnivorous, always with a prominent canine and two small accessories, the postcanines are simple conical teeth, the postfrontal is small and the occipital condyle single.

Family **Ictidosuchidae**

Upper Permian ictidosuchians linked to the alopecodontids.

The intertemporal region is narrow, usually with a sagittal crest and a pineal foramen present; primitively with a complete postorbital bar, but later incomplete; the coronoid process is prominent, the secondary palate absent, incipient to weakly developed; with an enlarged canine behind smaller accessories and the postcanines simple conical teeth, a single occipital condyle.

Family **Scaloposauridae**

Permian to Lower Triassic ictidosuchians.

Primitively with a narrow intertemporal region, but in some later forms this is widened and the pineal foramen is often absent.

Primitively with a complete postorbital bar, but later incomplete and sometimes even without a jugal spur.

The coronoid is weak or absent.

The secondary palate is incipient to weakly developed.

Primitively with an enlarged main canine, but in advanced forms not distinguishable, the postcanines are primitively conical but sometimes cusped.

SUBORDER BAURIAMORPHA

Triassic scaloposaurians further advanced than the ictidosuchians; the intertemporal region is narrow, usually with a sagittal crest and pineal foramen.

Postorbital bar, complete or incomplete.

Dentary with a prominent coronoid process; weak or robust with postdentary bones well developed or weak; with a well-developed closed secondary palate; epipterygoid moderately widened, lying lateral to braincase.

Incisors and canine conical or peglike, postcanines with cusps and transversely expanded. Occipital condyle notched or double.

Family **Bauriidae**

Intertemporal region narrow with sagittal crest; pineal foramen absent or present; the postorbital bar complete or incomplete, sometimes without jugal spur.

Dentary strong with well-developed postdentary bones. The vomer does not enter the secondary palate. Incisors and prominent canine conical and postcanines expanded.

Family **Ericiolacertidae**

Intertemporal region broadened, without sagittal crest, no pineal foramen; postorbital bar incomplete, without a jugal spur.

Dentary and postdentary bones lightly built.

The vomer enters the secondary palate.

No outstanding canine, incisors modified and postcanines peglike with cusps and expanded transversely.

ORDER CYNODONTIA

Advanced Upper Permian and Triassic gammatherapsids, derived from sphenacodonts probably through an intermediate stage at a morphological level near that of the Middle Permian therocephalians and scaloposaurians; including the ancestors of the mammals.

The intertemporal region is narrow with a sagittal crest, pineal foramen primitively present but later lost; postorbital bar complete in earlier forms but later incomplete. Dentary with weak to very strong coronoid process, the postero-ventral angle to the dentary is primitively weakly developed but very prominent in later forms; primitively without a posterior process but this is developed in later forms and in some forms reaches the squamosal to form an accessory articulation; the postdentary bones well developed in earlier forms but later much reduced. Primitively with a cleft secondary palate, but later closed.

The epipterygoid is widened and enters the sidewall of the braincase and becomes suturally joined to the prootic.

The dentition primitively with conical incisors and canines sometimes with accessory small canines; the postcanines developing cusps and later with widened variously elaborated crowns; primitively polyphyodont later diphyodont with 'premolars' and 'molars' distinguishable.

Postfrontal lost; no suborbital fenestra; occipital condyle notched and later double.

SUBORDER PROCYNOSUCHIA

Primitive Upper Permian and Triassic cynodonts, related to the two older gammatherapsid orders and linked to the first mammals.

Pineal foramen present and postorbital bar complete, zygoma lightly built.

In the dentary the postero-ventral angle is absent or only moderately developed; a masseteric fossa on the coronoid process is incipient to fairly well developed but there is still no masseteric process on the jugal; the posterior process of the dentary is still undeveloped; the postdentary bones are still well developed, but the reflected lamina of the angular is reduced. Initially the secondary palate is still cleft but is later closed.

The incisors and canine conical with accessory small canines sometimes present; accessory cusps on the postcanines.

Family **Procynosuchidae**

Upper Permian primitive procynosuchians still with a cleft palate, fairly weak coronoid process, with accessory precanine maxillary teeth; the occipital condyle is incipiently double.

Family **Galesauridae**

Upper Permian and Lower Triassic procynosuchians with a closed secondary palate, strong coronoid process without precanine maxillary teeth, and a double occipital condyle.

SUBORDER CYNOGNATHIA

Advanced specialized Triassic cynodonts, with a carnivorous and herbivorous branch, derived from Upper Permian procynosuchians, becoming extinct in the Upper Triassic.

Pineal foramen present, postorbital bar complete and a very strong zygoma.

Dentary greatly enlarged, prominent and strong coronoid process with masseteric fossa fairly to very well developed; strong to very strong postero-ventral angle; posterior process of dentary moderately to well developed and in some advanced forms making contact with the squamosal in an accessory articulation; masseteric process on jugal present or absent with a step between maxilla and jugal; postdentary bones greatly reduced with all but loss of reflected lamina of the angular. Secondary palate well developed and closed. Incisors and canines conical, without accessory anterior canines, postcanines with fore and aft accessory cusps or with crowns transversely expanded and further elaborated.

Family **Cynognathidae**

Earlier carnivorous cynognathians with the dentary not making contact with the squamosal, and with small angular process and jugal process; maxillary teeth divided into premolars with crenulated crowns and molars with a series of sectorial cusps in a longitudinal row.

Family **Chiniquodontidae**

Later carnivorous cynognathians with the dentary making contact with the squamosal in some advanced forms, usually no angular process to the dentary.

Family **Diademodontidae**

Earlier herbivorous cynognathians with very strong masseteric process on the jugal; long series of maxillary teeth with peg-like premolars and transversely widened crushing molars.

Family **Traversodontidae**

Later herbivorous cynognathians with a step between the maxilla and jugal and no masseteric process on the jugal.

SUBORDER TRITYLODONTIA

Advanced Upper Triassic cynodonts, derived from Upper Permian procynosuchians.

Without pineal foramen, postorbital bar incomplete without postorbital and postfrontal; zygoma very strong or fairly weak.

Dentary greatly enlarged with strong coronoid process and well developed masseteric fossa; postero-ventral angle very prominent, posterior process of dentary well developed and making contact with the squamosal in advanced forms; postdentary bones greatly reduced; no jugal process.

Secondary palate closed but greatly reduced in width with median shift of postcanines. Transverse ramus of pterygoid reduced.

Incisors primitively conical or specialized and recumbent, conical canine present or absent, postcanines cusped and further elaborated with crushing crowns.

Mononarial or binarial.

Family **Trithelodontidae**

Zygoma moderately strong; posterior process of the dentary not reaching the squamosal; incisors primitively conical, long diastema, long series of widened molars; mononarial.

Family **Tritylodontidae**

Zygoma strong; posterior process of the dentary not meeting the squamosal; incisors reduced, one enlarged, recumbent in dentary, no canine, long diastema, molars quadrangular with elaborate crushing crowns; mononarial.

Family **Diarthrognathidae**

Zygoma fairly weak; posterior process of the dentary making contact with the squamosal in an accessory articulation; incisors and canine primitively conical, no diastema, molars transversely widened with cusps; binarial.

Summary

The classification of the Therapsida is re-evaluated and the older view of two main branches, Anomodontia and Theriodontia, discarded in favour of three main branches for which the names Alphatherapsida, Betatherapsida and Gammatherapsida are proposed.

References

Boonstra, L. D. 1953. A new scaloposaurian genus. *Ann. Mag. nat. Hist.* (12) **6:** 601–605.

Boonstra, L. D. 1954. The cranial structure of the titanosuchian: *Anteosaurus. Ann. S. Afr. Mus.* **42:** 108–148.

Boonstra, L. D. 1963. Early dichotomies in the therapsids. *S. Afr. J. Sci.* **59:** 176–195.

Brink, A. S. 1963. The taxonomic position of the Synapsida. *S. Afr. J. Sci.* **59:** 153–159.

Broom, R. 1903. On the classification of the theriodonts and their allies. *Rep. S. Afr. Ass. Advmt Sci.* **1:** 286–294.

Broom, R. 1905. On the use of the term Anomodontia. *Rec. Albany Mus.* **1:** 266–269.

Broom, R. 1912. On some new fossil reptiles from the Permian and Triassic beds of South Africa. *Proc. zool. Soc. Lond.* **1912:** 859–876.

Broom, R. 1923. On the structure of the skull in the carnivorous dinocephalian reptiles. *Proc. zool. Soc. Lond.* **1923:** 661–684.

Broom, R. 1931. Notices of some new genera and species of Karroo fossil reptiles. *Rec. Albany Mus.* **4:** 161–166.

Broom, R. 1932. *The mammal-like reptiles of South Africa and the origin of mammals.* London: Witherby.

Efremov, I. A. 1940. Preliminary description of the new Permian and Triassic Tetrapoda from USSR. *Trudy paleont. Inst.* **10** (2): 1–140.

Efremov, I. A. 1954. [A fauna of terrestrial vertebrates in the Permian cupriferous sandstones of the western Ural region.] *Trudy paleont. Inst.* **54:** 1–416. (In Russian.)

Haughton, S. H. 1918. Investigations in South African fossil reptiles and Amphibia. (Part 11.) Some new carnivorous therapsids, with notes upon the brain-case in certain species. *Ann. S. Afr. Mus.* **12:** 175–216.

Haughton, S. H. 1924. A bibliographic list of pre-Stormberg Karroo fossils. *Trans. R. Soc. S. Afr.* **12:** 51–104.

Haughton, S. H. 1929. On some new therapsid genera. *Ann. S. Afr. Mus.* **28:** 55–78.

Huene, F. von. 1948. Short review of the lower tetrapods. *In* royal society of south africa. *Robert Broom commemorative volume:* 65–106. Cape Town: Royal Society of South Africa. (Special publication.)

Kutorga, S. 1838. *Beitrag zur Kenntniss der organischen Ueberreste des Kupfersandsteins am westlichen Abhange des Urals.* St. Petersburg: Eggers.

Lydekker, R. 1890. *Catalogue of the fossil Reptilia and Amphibia in the British Museum.* Part IV. London: British Museum.

Osborn, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Mem. Am. Mus. nat. Hist.* **1:** 449–507.

Owen, R. 1844. Description of certain fossil crania, discovered by A. G. Bain, Esq., in sandstone rocks at the south-eastern extremity of Africa, referable to different species of an extinct genus of Reptilia (*Dicynodon*) and indicative of a new tribe or sub-order of Sauria. *Proc. geol. Soc. Lond.* **4:** 500–504.

Owen, 1859 (1860). On the orders of fossil and recent Reptilia, and their distribution in time. *Rep. Br. Ass. Advmt Sci.* (Aberdeen, 1859) **29:** 153–166.

Owen, R. 1860. *Palaeontology; or, A systematic summary of extinct animals and their relations.* Edinburgh: Longman.

OWEN, R. 1876. *Descriptive and illustrated catalogue of the fossil Reptilia of South Africa in the collection of the British Museum.* London: British Museum.

REED, C. 1960. Polyphyletic or monophyletic ancestry of mammals, or: what is a class? *Evolution* **14**: 314–322.

ROMER, A. S. 1961. Synapsid evolution and dentition. *In International colloquium on the evolution of lower and non specialized mammals . . . September 1960.* **1**: 9–56. Brussels: Koninklijke Vlaamse Academie voor Wetenschappen, Letteren en Schone Kunsten van Belgie.

SEELEY, H. G. 1895. Researches on the structure, organization, and classification of the fossil Reptilia. Part IX, section 1. On the Therosuchia. *Phil. Trans. R. Soc.* (B) **183**: 311–370.

SIMPSON, G. G. 1925. A Mesozoic mammal skull from Mongolia. *Am. Mus. Novit.* **201**: 1–11.

TCHUDINOV, P. K. 1960. [Upper Permian therapsids of the Ezhovo locality.] *Paleont. Zh.* **1960** (4): 81–94. (In Russian.)

VAN VALEN, L. 1960. Therapsids as mammals. *Evolution* **14**: 304–313.

WATSON, D. M. S. 1917. Sketch classification of the pre-Jurassic tetrapod vertebrates. *Proc. zool. Soc. Lond.* **1917**: 167–186.

WATSON, D. M. S. & ROMER, A. S. 1956. A classification of therapsid reptiles. *Bull. Mus. comp. Zool. Harv.* **114**: 37–89.

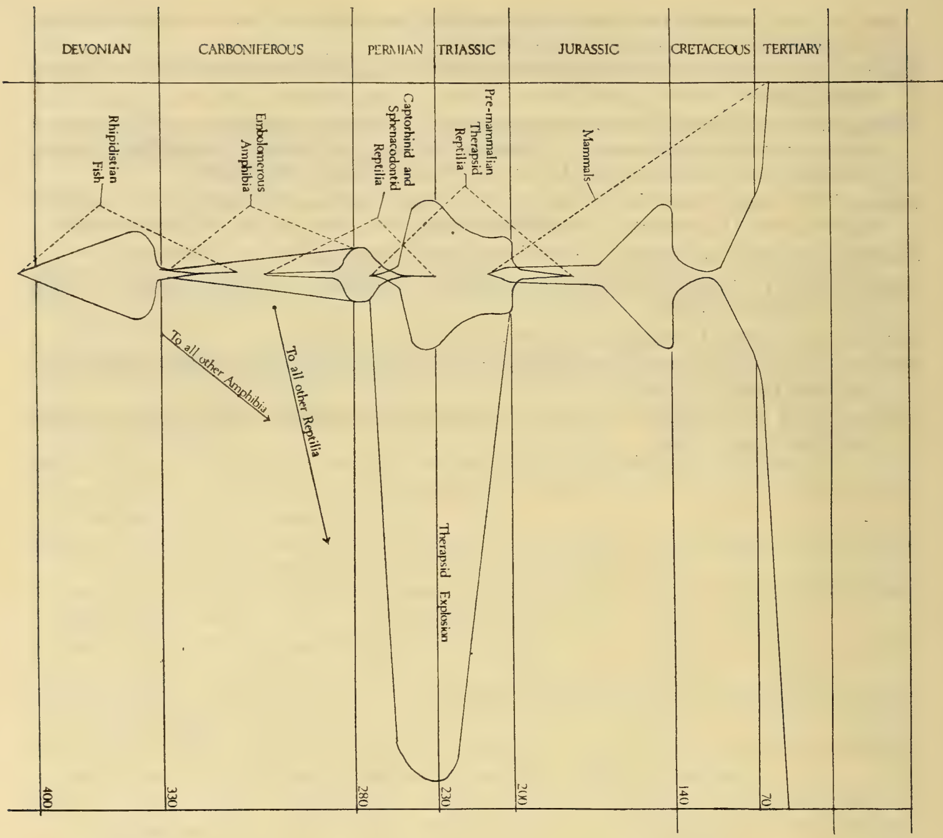

FIG. 1. Schematic representation of the evolutionary story of the mammals. The diagram is based on the number of described genera.

We commence the story nearly 400 million years ago.

At that time (the Devonian) there lived a group of freshwater fish, known as the Rhipidistia, whose paired fins had become adapted to propelling the body forwards with a purchase on the muddy floor of shallow pools.

These rhipidistians were succeeded (during the Carboniferous) by a group of amphibians, known as the Embolomeri, with two pairs of extremities capable of ungainly locomotion on dry land and with the ability of utilizing atmospheric oxygen but returning to the water for reproduction.

Just before the next period (the Permian) we encounter two groups of reptiles that had become completely adapted to life on land. These were the primitive Captorhinidae, with a simple adductor muscular mass for closing the jaw when feeding and the Sphenacodontia, where the adductor muscles had developed into a more efficient mechanism for feeding and able to raise the body from the ground for better locomotion.

Arising from these early reptiles (during the later part of the Permian) we have the Therapsida, which evolved in various directions, but with this in common viz. a great improvement in the jaw mechanism and locomotor ability. The majority of the therapsids, developing along differing but nearly parallel lines, became extinct, some in the Permian and others successfully competing to the end of the Trias.

Of the more successful therapsids we indicate in the scheme a group consisting of the familiar Scaloposauridae, Bauriidae, Tritylodontidae and Diarthrognathidae, brigading them together as the Premammalian Therapsida. In this group the locomotor ability is greatly improved and the jaw mechanism adapted more and more for chewing their food. For the latter the lower jaw became more and more dominated by a single bone—the dentary—and the teeth developed shearing, cutting and crushing cusps and the respiration during the chewing process was facilitated by the development of a bony secondary palate, separating the air passage from the buccal cavity.

Up to the end of the Triassic period all the vertebrates were poikilothermic or 'cold-blooded', i.e. they had no built in mechanism for temperature control. About this time certain of the higher therapsids, with their higher rate of metabolism, made possible by the improved locomotor and masticatory ability, developed mechanisms to dissipate excess body heat or to conserve it. For the former a skin with glands for sweating and a diaphragm for panting became imperative. To conserve heat the development of an insulating cover of hair or fur took place. These features, together with the dentary-squamosal jaw hinge made these small rat-like creatures mammals.

From their beginning late in the Triassic (about 150 million years ago) these first mammals were small rat-like animals forming a very inconspicuous part of the vertebrate fauna. This continued throughout the Jurassic and Cretaceous, when vertebrate life was dominated by the sauropsid reptiles which included the dinosaurs during their heyday.

But from the Tertiary the mammals waxed exceedingly to fill every possible ecological niche including besides terrestrial conditions varying from arctic to tropical climates, excursions into fresh and salt water and into the air. The culminating event, less than a million years ago, is the emergence of Man.

Since then this single genus has attained a dominant position in the living world, which it is ravaging at an alarming rate.

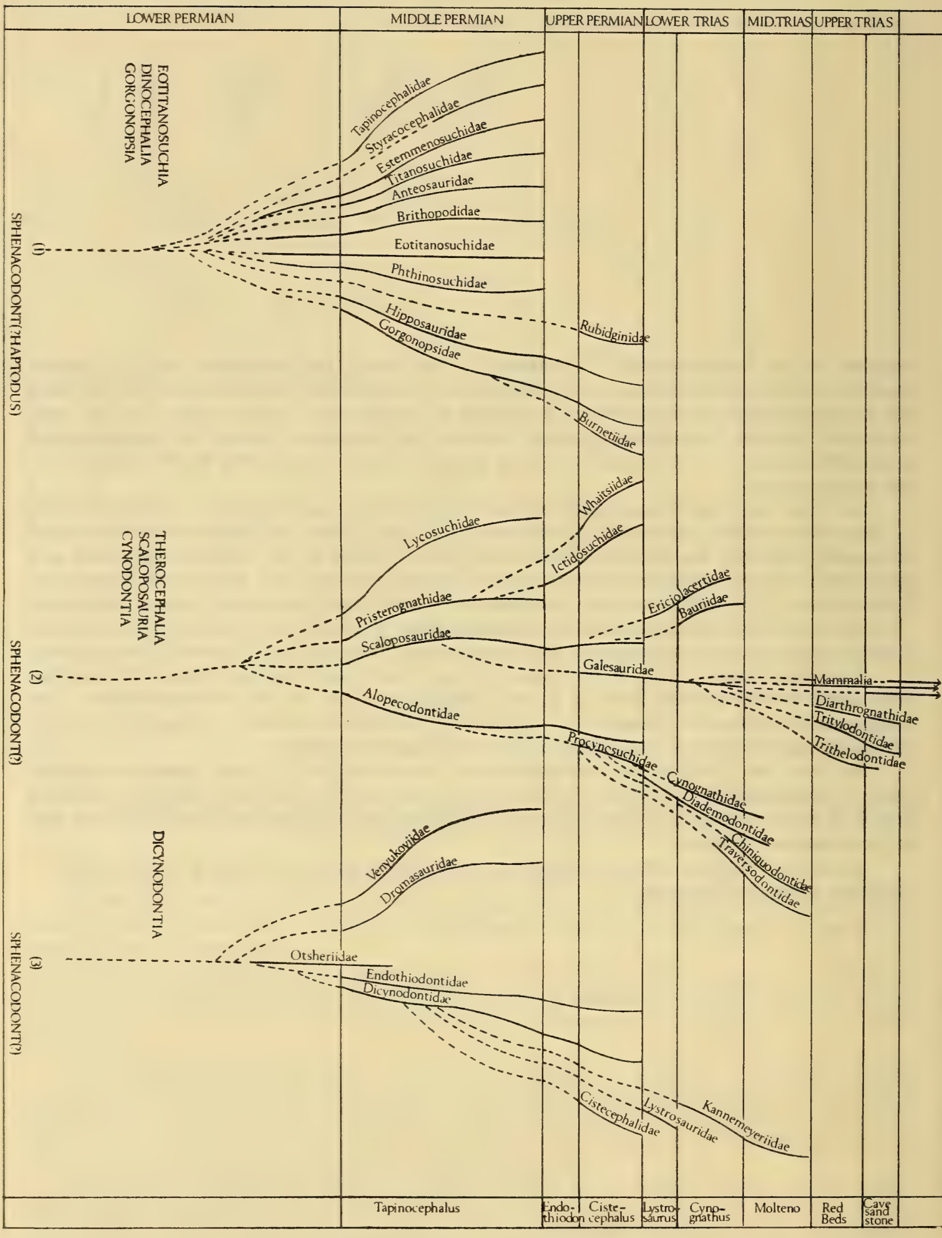

Fig. 2. Schematic phylogeny of the Therapsida.